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Eileen Hebets

University of Nebraska - Lincoln, ehébets2@unl.edu

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Attention-altering signal interactions in the multimodal courtship display of the wolf spider *Schizocosa uetzi*

Eileen A. Hebets

Department of Environmental Science, Policy and Management, Division of Insect Biology, 201 Wellman Hall, University of California, Berkeley, CA 94720, USA

Abstract

Complex signals are common throughout the animal kingdom, consisting of one or more signals in one or more sensory modalities presented within a single display. I tested an efficacy-based backup hypothesis of complex signal function using the bimodal courtship signaling wolf spider *Schizocosa uetzi*. This hypothesis predicts that the visual and vibratory courtship displays function as backups to each other in the presence of environmental variability. I compared mating frequencies across four environmental treatments in which the visual and vibratory environments were manipulated independently in a 2×2 design with visual treatments of light/dark (i.e., visual signal present/absent) and vibratory treatments of filter paper substratum/granite substratum (i.e., vibratory signal present/absent). Results did not match the predictions of an efficacy-based backup hypothesis. The vibratory environment affected mating frequency, with more mating occurring in the vibration-present treatments compared to the vibration-absent treatments, but the visual environment had no effect on mating frequency. A second experiment was then conducted to test for an inter-signal interaction. Using the video-playback technique, I presented females with manipulated video sequences simultaneous with a controlled vibratory signal to test the hypothesis that the presence of a vibratory signal alters a female's response to the visual signal. In the presence of a vibratory courtship signal, females were more receptive to more visually ornamented males. This increased receptivity to increased visual ornamentation was not seen in a previous study conducted on *S. uetzi* in the absence of a vibratory signal, suggesting a potential inter-signal interaction. In a third experiment, I tested whether a female's visual attention was altered by the vibratory signal by examining female response to a visual "predator" while exposed to all possible combinations of male courtship signals. Females were more likely to get caught, and thus less likely to notice a predatory visual stimulus when exposed to a courtship vibration, supporting the hypothesis that the vibratory signal alters a female's visual attention.

Keywords: attention-altering, complex signals, inter-signal interaction, limited attention, multimodal signals, spiders, video playback

Introduction

Signals form the building blocks of virtually all inter- and intra-specific communication. As such, signal evolution and design has received a great deal of attention, resulting in a remarkable amount of knowledge on signals in isolation or in taxa that are sensory specialists (animals which use predominantly one sensory modality) (e.g., vision: Andersson, 1982; Bischoff et al., 1985; Brooks and Caithness, 1995; Ligon and Zwartjes, 1995; acoustics: Bailey et al., 1990; Guilford and Dawkins, 1991; Ryan, 1980; Ryan and Rand, 1990). However, many displays throughout the animal kingdom are complex, incorporating more than one signal either within a single sensory modality (unimodal and typically multicomponent) or within more than one sensory modality (multimodal). Until recently the potential influence of multiple simultaneous signals on signal efficacy, information transfer, and ultimately signal evolution had received little attention (Candolin, 2003; Johnstone, 1996; Partan and Marler, 1999; Rowe, 1999).

Despite Partan and Marler's (1999) attempt to broaden views of multimodal signaling to include signal interactions involving dominance, modulation, or emergence, most currently tested hypotheses assume that signals act independently, and they focus exclusively on the information content, or message(s) conveyed, in individual signals (Johnstone, 1996). For example, the "multiple messages" hypothesis of Johnstone (1996) suggests that different signals convey different information about overall signaler quality, and several recent studies have found sup-

port for this hypothesis (Badyaev and Hill, 2000; Buchanan and Catchpole, 1997; Doucet and Montgomerie, 2003; Hankison and Morris, 2003; Kraak et al., 1999; Lindstrom and Lundstrom, 2000; McGraw and Hill, 2000). In contrast, the "backup" signal hypothesis (Johnstone, 1996) suggests that each signal is a partial indication of the signaler's overall condition and that a receiver benefits from multiple signals by increasing the accuracy with which they can assess a single quality. Tests of both hypotheses require knowledge of the information content of signals.

However, signal evolution is also influenced by the receiver's ability to receive and process signals (Dawkins and Krebs, 1978; Rowe, 1999). Just as individual signals evolve under both strategic (content-based) and tactical (efficacy-based) selection pressures (Guilford and Dawkins, 1991), so must complex signals. In this paper, I first test an efficacy-based backup hypothesis of complex signaling. Pure efficacy-based hypotheses predict only differences in the probability of receiver response, making no assumptions about information content or receiver benefits. For example, an efficacy-based backup hypothesis proposes that different signals may be more easily detected or discriminated under different environmental conditions and, thus, combining multiple signals may allow a signaler to overcome environmental variability. This hypothesis is especially intuitive when thinking of multimodal signals: given increased environmental noise in signaling modality "A," a receiver is still able to detect signal "B," which is transmitted via a different modality and vice versa. This efficacy-based backup hypothesis predicts that across all environmental conditions, the probability of a receiver responding to

a multiple signal "A,B" will be greater than the probability of responding to either signal "A" or signal "B" alone. It can be empirically tested without any a priori knowledge of the information content of individual signals. An assumption of this hypothesis, however, is that each signal acts independently to produce the same type of response: that the presence of one signal does not alter a receiver's response to a second signal, resulting in an inter-signal interaction. Hypotheses involving inter-signal interactions comprise a relatively unexplored, yet potentially extremely important category of hypotheses (Candolin, 2003).

Schizocosa wolf spiders provide an excellent system in which to test hypotheses of complex signal evolution and function. Species in this genus exhibit a wide spectrum of simple to complex courtship signaling, with species displaying unimodally (vibratory signal only) as well as bimodally (a vibratory signal plus a visual signal). Although chemical and tactile signals could be important in this group, visual and vibratory signals are the most obvious modalities used by *Schizocosa* during courtship, and thus I chose to focus on these two for this study. The visual courtship signals often consist of both a movement (i.e., leg waving, leg arching, body bounce, etc.) and an associated elaborate foreleg ornamentation that has been suggested to enhance the movement (Hebets et al., 1996; Hebets and Uetz, 1999, 2000; Scheffer et al., 1996; Stratton and Uetz, 1981, 1983, 1986; Uetz and Denterlein, 1979). The combination of movements and ornamentation makes the visual signal multicomponent. No species that we know of uses only a visual signal. Previous studies exploring signal evolution within this genus have compared patterns of female receptivity to isolated and combined conspecific courtship signals across multiple species (Hebets and Uetz, 1999; Scheffer et al., 1996). While these results can be used preliminarily to explore some functional hypotheses of complex signal evolution, no such hypotheses have been explicitly tested.

Here I first test the efficacy-based backup hypothesis in *Schizocosa uetzi* by allowing pairs of males and females to interact, and thus potentially copulate, under four environmental treatments. I used a 2×2 design to independently manipulate the visual and vibratory environments and assessed mating frequency. Results from this initial experiment did not support an efficacy-based backup hypothesis. In a second experiment, I used video playback to test whether the presence of a vibratory signal altered a female's response to manipulated visual signals. Results of this experiment suggested an inter-signal interaction. In a third experiment, I tested the hypothesis that the presence of a vibratory courtship signal alters a female's visual attention.

Materials and Methods

Schizocosa uetzi males have black pigmentation over the middle portion of the tibia of their forelegs and use a courtship display consisting of a stationary stridulation with an intermittent slow foreleg arch (Stratton, 1997). Mature female *Schizocosa uetzi* were collected at night from three sites in Lafayette and Marshall Counties in northern Mississippi, USA, between July 4 and July 5, 1995 for the video playback experiments. Immature males and females were collected during the day and at night from two sites in Panola and Lafayette Counties in northern Mississippi, USA, in late May 2000 and 2003 for the efficacy-based backup and attention-altering hypothesis experiments. All spiders were brought back to the laboratory where they were housed individually, provided with a constant source of moisture, and fed 3–5 crickets once a week.

Females were already mature when collected in 1995, so their sexual history was unknown and thus they could not be used in receptivity trials. Twenty-nine of these females produced egg sacs, from which spiderlings were raised in the laboratory. Once mature, spiders from different egg sacs were used in the video playback trials. In 2000 and 2003 all females were collected as immatures and thus were known to be virgins when they matured in the lab.

Efficacy-based backup hypothesis

This experiment was a fully crossed 2×2 design with a visual treatment of light versus dark and a vibratory treatment of filter paper substratum versus granite substratum. Since this experiment relies on natural behaviors, I did not manipulate individuals to eliminate a signaling or receptive modality (for example, inhibiting the movement of the male pedipalps to eliminate the use of the stridulatory organ used to produce the vibratory signal, or covering the eyes of females to eliminate the reception of visual signals). Manipulating the environment through which each signal traveled was the most unobtrusive way to alter the signal's reception by a receiver without altering signaler behavior. An earlier experimental design was modified in a second try. All light treatments were run under artificial laboratory lighting while dark treatments were run in a dark room and were observed through the viewing window of a Sony DCR-TRV38 MiniDV Handycam Camcorder using the nightshot option. The vibratory signal was removed by using granite as the substratum upon which males courted. Using a laser vibrometer, it has been demonstrated that at a zero measurement point (i.e., immediately in front of the signal source), a seismic signal decreases by 60 dB, a 10^3 decrease in signal intensity. Granite therefore, is a substratum through which seismic signals effectively do not travel (Elias D, unpublished data). For the vibration-present treatment, filter paper was used as the courting substratum. Minimal-vibration arenas were built using a glue gun to attach circular acetate arenas measuring 10.1 cm in diam to the surface of a smooth piece of granite (Figure 1b). The surface of the granite inside the arena was painted with white paint to control for background color. In vibration-present arenas, the same sized circular acetate arenas were placed inside a $10.16 \times 10.16 \times 12.86$ cm Amac Plastic Product clear box (Figure 1a). The bottoms of the boxes were painted with the same white paint as the rocks to control for any odor effects of the paint and a piece of filter paper lined the bottom of the arena, providing a surface on which males could court.

All females were virgins and had molted to maturity in the laboratory at least 10 days prior to the trial. Seventy-four males and 74 females were each only used once. Females were randomly assigned to one of the four environmental treatments. Females were placed in their assigned arena and were allowed to acclimate for 2 min, after which time a randomly assigned male was introduced. During a set of trials, two treatments were run simultaneously, each with two replicates. A set of trials was run either in the light or in the dark, with two replicates of filter paper substratum and two replicates of granite substratum. Trials lasted one hour and were observed continually for the presence/absence of male courtship behavior; presence/absence of copulation; and when copulation occurred, the latency to copulation.

Inter-signal interaction hypothesis

This experiment used video playback to test the hypothesis that

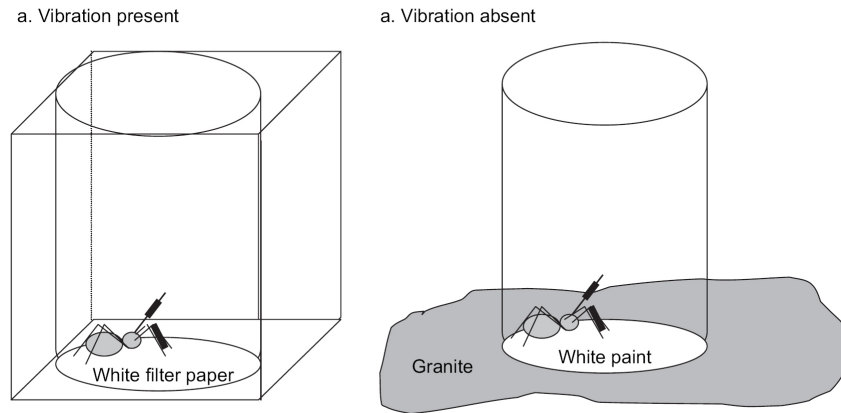


Figure 1. Experimental arenas for the efficacy-based backup experiment. **(a)** A circular acetate arena is placed inside a plastic box which has its bottom painted with white paint. Filter paper lines the bottom of the arena and acts as the courting substratum (i.e., vibration-present treatment). **(b)** A circular acetate arena is glued to the surface of a large, flat piece of granite, which provides the courting substratum (i.e., vibration-absent treatment). The surface of the granite is painted white, providing a similar background between treatments.

the presence of a vibratory signal alters a female's response to a visual signal. Video imaging allows for phenotypic manipulation independent of behavior (Clark and Uetz, 1990, 1992), and this powerful tool was used in a previous study to assess female *S. uetzi* responses to video playbacks of courtship sequences of males with manipulated foreleg morphologies (Hebets and Uetz, 2000). A total of three video courtship sequences were created and tested with mature virgin females: (1) a "brushes" video: brushes of black hair were added to the male forelegs; (2) a pigment only video: an unaltered video sequence; and (3) a no ornamentation video: black pigmentation was removed from the forelegs (Hebets and Uetz, 2000). Hebets and Uetz (2000) used these videos to assess *S. uetzi* female receptivity in the absence of a vibratory signal. Using the same digitized video sequences and four of the same nine spiders, I was able to examine female responses to these video playbacks in the presence of a courtship vibration. The present study was conducted a few weeks after the previous study (Hebets and Uetz, 2000). An arena was constructed that allowed for the simultaneous perception of a live male courtship vibration and a visual video playback stimulus. A Sony Watchman microscreen television was placed at one end of a clear plastic arena. A cut was made along the bottom edge of the arena that allowed a piece of filter paper to provide a continuous substratum from within the arena to the shelf outside (Figure 2). A visual barrier (opaque paper) on the one side of the arena prevented females from seeing the live male. A male was placed in a small circular acetate chamber (~1.5 cm diam) that contained a piece of filter paper removed from a mature female's cage. The presence of female silk on the paper stimulates a male to court in isolation.

Preliminary trials assured that the vibrations could travel from the shelf to the test arena by testing females that had been receptive previously to vibrations alone in related experiments. These females showed receptivity without the video stimulus within a 10-min period, indicating reception of male vibratory signals through the substratum. All females were chosen at random and each female was shown three different videos representing three different male foreleg morphologies (a male with foreleg "brushes," with pigment only, and with no ornamentation).

Only one male provided the vibratory signal for every female and video stimulus. Visibly, the courtship of this male did not vary in any obvious way across hours or days. Although this methodology did not control for possible male fatigue or intra-

individual variation, it was the best way to control for variation among males in their vibratory signals. Ideally, I would have used different males for each female with sample sizes triple what I had; however, due to small numbers of available spiders, using the same male across treatments seemed the best way to control the vibratory signal. To help control for potential male variability over time, the order in which the video stimuli were presented to each female was random as was the order in which females were tested. One 10-min trial was performed per female on each of three consecutive days, and females were scored as receptive or unreceptive.

Female receptivity was scored according to the presence/absence of three distinct behaviors: (1) a "slow" turn: a slow, deliberate 90° to 180° turn away from the male; (2) a "settle" near the male: a flattening of the entire body along with a stretching out and lowering of all walking legs; and (3) an abdomen bob in which the female repeatedly dips her abdomen towards the ground. Past research with *Schizocosa* females has utilized

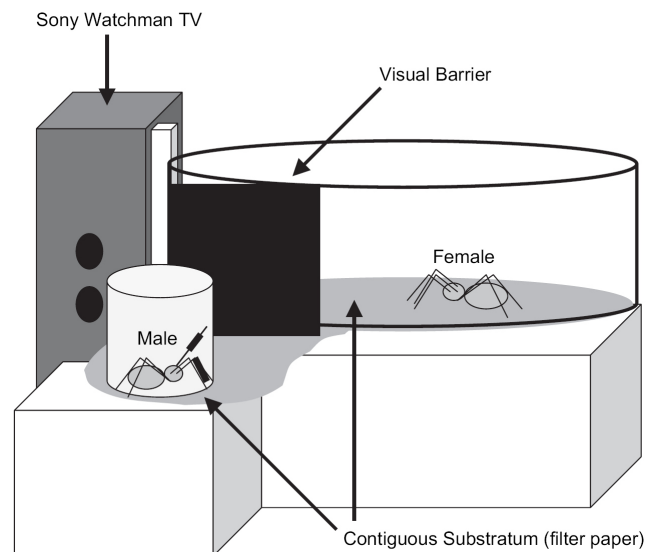


Figure 2. The experimental arena used for the inter-signal interaction experiment using video playback. A live male provided courtship vibrations to a female that was exposed to manipulated video sequences played back on a Sony Watchman television.

similar measures of female receptivity (Hebets and Uetz 1999, 2000; McClintock and Uetz 1996; Scheffer et al., 1995; Stratton and Uetz 1981, 1983). If the female showed at least one of the above-mentioned displays during her 10-min trial, she was scored as receptive.

As females were used more than once, a repeated measures Cochran's Q test was used to analyze this as a randomized block experimental design with dichotomous variables (receptive/unreceptive). Given that the Cochran's Q test was significant, a McNemar's test of a two-by-two contingency table with dichotomous data determined the source of the differences.

Attention-focusing interaction hypothesis

I next tested a female's ability to respond to a predatory visual stimulus while she was exposed to one of four courtship treatments: (1) a courtship display including both visual and vibratory signals, (2) a visual courtship signal in isolation, (3) a vibratory courtship signal in isolation, and (4) no courtship signal.

Two separate arenas were used for this experiment, one for scenarios 1 and 3 (vibrations present) and one for scenarios 2 and 4 (vibrations absent). For the vibration-present treatments, a 4-in \times 8-in arena was used. Two different partitions were made to be placed in the center of the arena separating it into two 4-in \times 4-in halves. One partition was clear transparent acrylic enabling visual signals to pass while the other was solid white and removed all visual signals. A single piece of filter paper covered the bottom of the entire arena, forming a contiguous surface from one side to the other so that vibrations could be transmitted unhindered. Females were placed on one side of the arena and males on the other.

For trials in which no vibration was present, two 4-in \times 4-in arenas were used. The arenas were placed against each other so that one entire wall was juxtaposed to the wall of the other but they were not touching. These arenas were made of clear plastic acrylic (Amac Plastic Products) such that the spiders could easily look into the other arena. Each arena sat on top of separate pieces of isolating foam in order to prevent the transmission of vibrations (Hebets and Uetz, 1999; Scheffer et al., 1996). Males were placed in one arena while females were in the other. Thus, females could see a male but were not able to detect his vibrations. In cases in which there was no signal, females were simply tested in one of the arenas and the other arena was left empty.

The order in which females were run through the four treatments was random. Females were placed in their appropriate arena first and allowed to acclimate for one min, after which time males were introduced. Trials began when a male started courting. After two min in the treatment condition, the female was confronted with a visual stimulus simulating a predator.

The "predator" was a glass vial with the bottom painted black and a strip of orange around the lip. There was no significance to the color combinations chosen; it was simply used to add contrast to the clear glass. The vial was lowered directly on top of the female at as constant a rate as possible from a height of 4 in. Experimental design and female behavior did not allow for an automated predator.

Initially, I held the vial above the females and attempted to lower it at a constant rate in an attempt to capture the female. Two naïve undergraduate students who were unaware of the purpose of the experiment then did vial presentation. The assistants were instructed to hold the vial 4 in above a female and on my signal (i.e., after 2 min of exposure), were asked to lower the vial on top of the female at a constant rate to attempt to catch her. Females were ei-

ther captured under the vial when the vial reached the floor of the arena or they were not. Each student conducted a series of trials for only one day and recorded whether or not the female was captured.

Results

Efficacy-based backup hypothesis

Across all treatments, pairs mated most frequently in the light when vibrations were detectable (35%), followed by in the dark with vibrations detectable (22%), and the lowest frequencies occurred in both treatments with vibrations masked (both 5%). Mating frequency was dependent on environmental treatment ($N = 74$, $\chi^2 = 8.68$, $p = .034$). When separating out the effects of the environmental treatments, mating frequency was dependent on the vibratory environment ($\chi^2 = 7.9$, $p = .005$) but not on the visual environment ($\chi^2 = 0.4$, $p = .53$), with more mating occurring in the vibration-present versus vibration-absent treatments. While the sample sizes for copulations across treatments are relatively low, the latency to copulation does not appear to differ among the treatments (light/vibration $N = 6$, mean = 18.89, SE = 5.3; light/no vibration $N = 1$, duration = 10.5; dark/vibration $N = 4$, mean = 17.42, SE = 6.5; dark/no vibration $N = 1$, duration = 0.25).

The above results are for all trials, independent of whether or not the male engaged in courtship. However, I found that the presence/absence of male courtship was also dependent on environmental treatment ($N = 74$, $\chi^2 = 15.2$, $p = .0017$). Males courted 100% of the time in the light, vibration-present treatment and 90% of the time in the light, vibration-absent treatment. However, males only courted 61% of the time in the dark, vibration-present treatment and 63% of the time in the dark, vibration-absent treatment. When separating out the effect of environmental treatments, I found that males courted significantly more in the light than in the dark ($\chi^2 = 12.63$, $p = .0004$) but that the presence/absence of vibration had no effect on the presence/absence of male courtship ($\chi^2 = 0.103$, $p = .75$).

In analyzing only the trials in which a male engaged in courtship, I found the same pattern as when combining all the trials. Mating frequency was dependent on environmental treatment ($N = 58$, $\chi^2 = 8.04$, $p = .045$; Figure 3), and when separating out the effects of the treatments, mating frequency was dependent on the vibratory treatment ($\chi^2 = 5.9$, $p = .015$) but not the visual treatment ($\chi^2 = 0.08$, $p = .77$; Figure 3), with more mating occurring in the vibration-present than vibration-absent treatments.

Inter-signal interaction hypothesis

A total of 10 *Schizocosa uetzi* females were exposed to three different video manipulations. Four of the females were used in a similar previously published experiment using visual stimuli only (Hebets and Uetz, 2000). One of these four females was unreceptive to the control video without vibration (Hebets and Uetz, 2000) and receptive when vibration was added (present study). A second female was receptive to a brushes video with no vibration (Hebets and Uetz, 2000) and unreceptive to a brushes video with vibration added (present study). The other two females responded identically to the stimuli in both experiments (control – /–; brushes +/+). In the presence of a vibratory signal, a *S. uetzi* female's response to video stimuli was dependent on the stimulus shown ($Q = 9$, $p < .05$; Figure 4, black bars; white bars represent results from Hebets and Uetz [2000], $N = 9$). Female receptivity was significantly greater to stimuli of enhanced males than to stimuli of males with no ornaments ($\chi^2 = 4.16$, $p < .05$). Al-

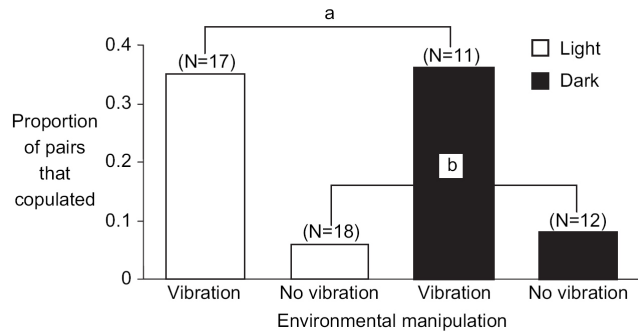


Figure 3. The proportion of pairs that copulated across the four environmental treatments, analyzing only trials in which the male engaged in courtship ($N = 58$). Mating frequency did depend on environmental treatment ($\chi^2 = 8.04$, $p = .045$). Separating out the effects of environmental treatment indicates that mating frequency depends on the vibratory environment ($\chi^2 = 5.9$, $p = .015$) but not on the visual environment ($\chi^2 = 0.08$, $p = .77$). Significant differences are indicated by unshared letters.

though Figure 4 indicates a trend for females to respond to control stimuli more strongly than to stimuli of males with no ornaments, females in the control trials did not differ significantly from either treatment (no ornament: $\chi^2 = 1.33$, $p > .05$; brushes: $\chi^2 = 1.33$, $p > .05$; Figure 4).

Attention-altering interaction hypothesis

A total of 38 females were run through the attention-altering trials: 12 females were run through trials in which I lowered the vial, while the remaining 26 females were run through trials in which assistants lowered the vial. Sixty-eight percent of the females altered their response among treatments ($N = 26$). A Cochran's Q repeated measures analysis for dichotomous variables was conducted to determine if female response varied with treatment. The test statistic Q is not affected by having blocks that contain all of the same response and, thus, the 12 females that did not vary in their response among treatments were removed from the analysis (Zar, 1999). When data were separated into those that I collected, those that my assistants collected, and all data combined, Cochran's Q analyses revealed that female response did depend on treatment but not on experimenter identity (my data: $Q = 30.5$, $df = 3$, $N = 10$, $p < .001$; assistant's data: $Q = 11.03$, $df = 3$, $N = 16$, $p < .03$; all data combined: $Q = 15.27$, $df = 3$, $N = 26$, $p < .005$). Thus, all following analyses include all data combined. Females were most likely to get caught when both signals were present (69%), followed by vibration only (61%), followed visual only (44%), and they were least likely to get caught when there was no male signal present (29%) (Figure 5). A McNemar's test on pairwise comparisons revealed that females were more likely to be captured when exposed to both signals combined compared to only visual signals (visual, vibration vs. visual, no vibration: $\chi^2 = 4.27$, $p < .05$; Figure 5) but not compared to only vibratory signals (visual, vibration vs. no visual, vibration: $\chi^2 = 0.64$, $p > .05$; Figure 5). There was no difference in female capture frequencies when treatments of each signal in isolation were compared (visual, no vibration vs. no visual, vibration: $\chi^2 = 0.94$, $p > .05$; Figure 5). Female capture rate in the absence of any signal was lower than when only a vibratory signal was present (no visual, no vibration vs. no visual, vibration: $\chi^2 = 5.06$, $p < .03$; Figure 5) but not when only a visual signal was present (no visual, no vibration vs. visual, no vibration: $\chi^2 = 1.78$, $p > .05$; Figure 5).

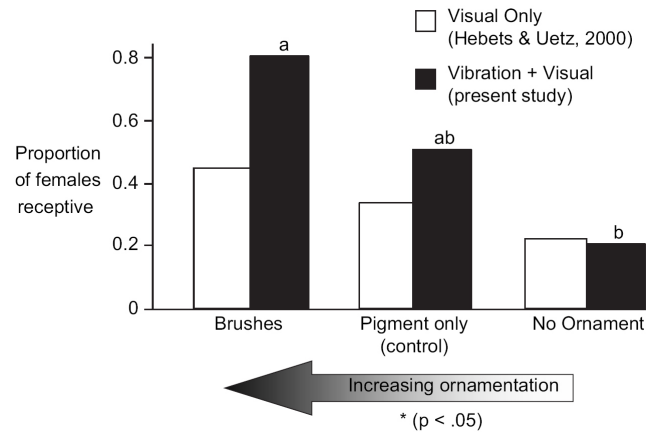


Figure 4. The proportion of females receptive to manipulated courtship sequences. White bars represent data from a previous study assessing female receptivity to visual signals in isolation (Hebets and Uetz, 2000). Black bars represent results from this study, which combines manipulated visual signals with a vibratory signal. Female receptivity was dependent on the visual stimulus in the present study ($\chi^2 = 1.33$, $p < .05$), and pairwise comparisons reveal that the difference is between receptivity to the brushes video versus the no ornamentation video. Significant differences are indicated by unshared letters.

In an analysis combining all vibration-present/absent treatments and all visual-present/absent treatments, females were more likely to be captured when a vibratory signal was present versus absent ($\chi^2 = 14.098$, $p = .0002$; Figure 5), but the presence/absence of a visual signal did not affect female capture frequency ($p > .05$). In a log-likelihood test that does not account for repeated measures, I find the same results ($\chi^2 = 17.38$, $p = .0006$; visual $\chi^2 = 2.87$, $p = .09$; vibration $\chi^2 = 13.63$, $p = .0002$; visual \times vibration $\chi^2 = 0.31$, $p = .58$).

Discussion

Results from the first experiment in this study, which assessed mating frequency under different environmental conditions, do not support the predictions of the efficacy-based backup hypothesis. In the absence of a vibratory signal, even in the presence of a visual signal, females responded as if no signal were present (Figure 3), suggesting that the vibratory signal is critical for successful mating in this species and that the visual signal is not sufficient. Furthermore, even in complete darkness, as long as a

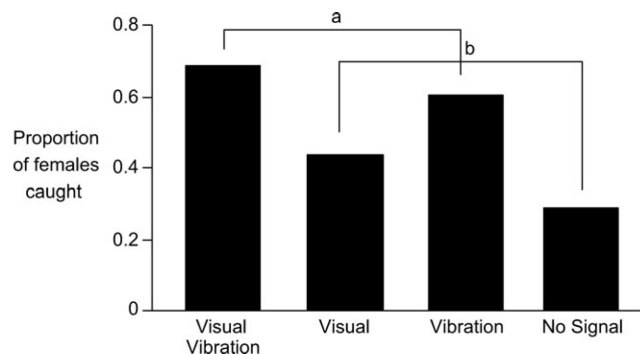


Figure 5. Proportion of females caught while exposed to various combinations of male courtship signals ($N = 26$). Females were more likely to get caught when a courtship vibration was present than when it was absent. Different letters indicate significant differences of $p < .05$.

vibratory signal was present, the mating frequency equaled that of light conditions, resulting in no decrease in the probability of mating, given only one signal. As opposed to the signals acting as backups to each other, results from this first study suggest that the vibratory signal may be dominant to the visual signal. Although the visual stimulus of a female is important in eliciting male courtship, the visual stimulus of a courting male is not sufficient for successful mating.

The efficacy-based backup hypothesis assumes that signals are independent and, thus, the second experiment explored a potential inter-signal interaction. Specifically, I was interested in how females respond to visual stimuli in the presence of a courtship vibration. Using video playback to present females with real-time courtship displays of males with manipulated foreleg morphologies simultaneous with a live male courtship vibration, I found that *S. uetzi* females increase their receptivity to more visually ornamented males. To appreciate the implications of these results, it is important to evaluate them in light of a previous study in which female receptivity to these identical manipulated video sequences was measured in the absence of a vibratory signal (Hebets and Uetz, 2000; Figure 4, white bars). In the previous study, while there was a slight trend for females to increase in receptivity with increased male ornamentation, this trend was not significant (Hebets and Uetz, 2000). However, in the present study, when a vibratory signal is added, females almost double in their receptivity to the brushes-added video, resulting in a significant difference in receptivity between the no ornamentation and brushes-added stimuli. Unfortunately, while these two studies were conducted in the same year, they had different experimental designs and thus are impossible to compare directly. In 2000, Hebets and Uetz used females only once and thus analyzed their data using a G test. In the present study, a repeated measures design was used, as each female was tested with each video sequence. The difference in experimental design does not allow for direct comparison or combined analysis. While four of the females from the 2000 study were used for the present study, only two of them altered their response to their initially viewed video sequence. One female, having previously displayed no receptivity, showed receptivity to a control video with vibration added. A second female was not receptive to a brushes video with vibration added, having shown receptivity previously. Using females in this study a few weeks after Hebets and Uetz (2000) actually results in a conservative estimate of female receptivity since females tend to decrease in receptivity with age (E. A. Hebets, personal observation). Ultimately, while these results are very suggestive of an inter-signal interaction in which the vibratory signal alters a female's response to the visual signal, to demonstrate it conclusively a study should be conducted in which the vibration/no vibration treatments are combined into one experiment and directly compared.

Nonetheless, the results from this second experiment suggest that females may be paying more attention to a visual signal in the presence of a vibratory signal. The term attention refers to the information processed by an organism at any given time, and it has been demonstrated in a wide variety of animal taxa, including humans, that there is a constraint on the ability to process all possible sensory information; this is referred to as limited attention (for review see Dukas, 2002). Due to limited attention, organisms often find ways of filtering out unnecessary sensory stimuli. While engaged in difficult tasks, for example, it has been shown that performance can be increased by focusing attention as opposed to dividing it among tasks or locations (reviewed in Dukas, 2002). The third experiment in this study tests the idea that one signal (the vibratory signal) can alter or focus a receiver's attention towards

a second signal (the visual signal), thus potentially overcoming problems associated with limited attention. To test this attention-altering hypothesis, I used an experimental design similar to those used in testing limited attention of foraging and simultaneously attending to predators (Creswell et al., 2003; Dukas and Kamil, 2000, 2001; Kaby and Lind, 2003). Instead of using foraging, I tested a female's ability to simultaneously attend to a potential mate and a potential predator. If the vibratory signal indeed alters a female's visual attention, then the presence of a vibratory signal should alter a female's susceptibility to a visual predator. My results demonstrate just that: females are caught significantly more in the presence of a male courtship vibration than in its absence (Figure 5). The presence of a courtship vibration made females less sensitive to predatory visual stimuli, suggesting a tradeoff between attending to potential mates versus to potential predators. While evidence of limited attention has been documented in several taxa, including blue jays, where a bird's ability to detect a peripheral target is decreased when it is focused on a foraging task (Dukas and Kamil, 2000), until now, it has not been studied in the context of courtship and mate choice.

Due to limited attention, animals often filter available information in one of two ways: (1) stimulus-selective attention, where a receiver can attend to a subset of available stimuli, ignoring all others and (2) spatially-selective attention, where a receiver can focus attention on a small portion of a particular sensory stimulus, for example, a small portion of the visual field (Dukas, 2002). Attention-altering by means of selective-attention would suggest that in the context of mate choice, vibratory perception in *S. uetzi* dominates visual perception and that when a female is paying attention to vibratory signals, she cannot, or does not, pay attention to other sensory stimuli. In the first experiment of this study, mating frequency did not differ between light and dark treatments as long as a vibratory signal was present, supporting a dominant role of the vibratory signal. However, results from the video playback experiment demonstrate a more complex interaction between the signals than a simple dominance relationship would predict. Selective-attention need not filter out sensory stimuli in neat categories such as via modalities, but it could filter out all information that does not fit a generalized form. For example, the presence of a vibratory signal may invoke a visual search image in the female, targeting her visual attention on specific stimuli relating to a courting male. Being visual hunters, wolf spiders rely heavily on visual cues for prey capture and detection (Persons et al., 1999; Persons and Uetz, 1996, 1999). If a female relies predominantly on vision for foraging, she may not immediately distinguish a courting male from prey. A vibratory signal that could redirect her visual attention and focus it may be useful, and it may decrease the likelihood of sexual cannibalism. Unfortunately, the experiments in this study cannot address these hypotheses and future studies are necessary to distinguish among them.

The second means by which females could filter information is attention-altering via spatially-selective attention. In this system, a vibratory signal could focus a female's visual attention on a small portion of the visual field. For example, in *S. uetzi* spatially-selective attention could result in a visual focusing on the horizontal plane, ignoring all visual stimuli from above. Under this scenario, females would be more susceptible to an aerial predator in the presence of a courtship vibration (as seen in this study) but would readily escape from a terrestrial predator. This study only focused on aerial predators, but using a similar design to test for susceptibility to terrestrial predators would be fruitful in distinguishing among the mechanisms of attention-altering.

Krause and Godin (1996) found that foraging posture affected an individual guppy's ability to respond to an approaching predator. Following from this, an argument could be made that a female wolf spider's body position could have influenced her ability to escape the capture vial in the attention-focusing experiment. However, the presence or absence of a courtship vibration did not affect a female's body position in any obvious way, based on casual observations. The vial always came down directly above a female, and thus her body position and orientation should not have affected her ability to escape. Another possibility, however, is that a vibratory courtship signal could decrease a female's perception of disturbances in air currents caused from lowering the vial, resulting in stimulus-selective attention in which a female's vibratory perception is dominant to her mechanosensory perception. The substratum-borne vibrations of the male courtship signal are detected through sensory organs consisting of slits in the female's cuticle (slit sensilla), and airborne vibrations are detected through sensory hairs located on the legs (trichobothria). While signals in these differing channels are received peripherally by different sensory organs, it has been shown in another spider (*Cupiennius salei*) that there is convergence of the afferents from these different sensory modalities, creating the possibility of a functional interaction in behavior (Barth, 2002). Future research exploring this possibility in *S. uetzi* is necessary before this hypothesis can be addressed.

While my results support an attention-altering hypothesis for the multimodal signaling wolf spider *S. uetzi*, it is important to note that the results are not inconsistent with a content-based multiple messages hypothesis, and these hypotheses are not mutually exclusive. The visual and vibratory courtship signals may provide different types of information to a female. The vibratory signal initiates courtship in *S. uetzi* and the visual signal is subsequently added, consistent with the possibility that the vibratory signal provides directional information while the visual signal provides information about the signaler's quality, a multipart message representing different types of information. However, under this functional scenario, one would predict mating frequencies to be lower in the dark than in the light, since females would not be able to assess the visual quality indicator. My results indicate no significant difference in mating frequency based on visual treatment (Figure 3). One would also predict latency to copulation to be shorter in the light, vibration-present treatment as compared to the light, vibration-absent treatment, and my results do not support this prediction either. Furthermore, this multiple messages hypothesis does not predict the video playback results, since the vibratory and visual signals were not spatially matched. Nonetheless, if a vibratory signal provides directional information, and females respond by directing their visual field towards a courting male in order to assess a quality-indicating visual signal, ultimately, the vibratory signal focuses a female's attention on the visual signal. Thus, the precise way in which a female's attention may be altered could be explained in part by the information content of the vibratory signal, an explanation that does not require one to invoke the notion of limited attention or constraints on receiver information processing. However, in the absence of knowledge regarding the information contained in each signal, it is currently difficult to assess the importance of content-based hypotheses in this system. Again, the efficacy-based attention-altering hypothesis and the content-based multiple messages hypothesis are not mutually-exclusive, and both may have played an important role in the evolution of the multimodal courtship displays of *S. uetzi*.

In conclusion, this study rules out the possibility that the visual and vibratory courtship signals of *S. uetzi* act simply as backups to each other in the presence of environmental variability. My results instead suggest that the signals are not independent and that they interact in such a way that the vibratory signal alters the receiver's response to the visual signal and that this is likely achieved by altering a receiver's visual attention. Our past and much of our current empirical work on signal evolution has assessed signals in isolation and has assumed signal independence. By conducting experiments in a way that does not allow for possibilities of inter-signal interactions, results obtained may have little relevance to natural signal functions. This study makes it clear that our focus needs to broaden and allow for the possibility of inter-signal interactions and that through understanding these interactions we may be led to new hypotheses relating to complex signal evolution.

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